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BIOLOGICAL BULLETIN

A CRUSTACEAN-EATING ANT (LEPTOGENYS ELONGATA BUCKLEY).

WILLIAM MORTON WHEELER.

There are few more profitable fields for the comparative study of instinct than the larger genera of the social Hymenoptera. This is especially true of the larger genera of ants, such as *Camponotus*, *Formica*, *Myrmecocystus*, *Leptothorax*, *Pheidole*, *Atta* and *Crematogaster*. To these genera, each of which embraces species presenting a considerable range of ethological peculiarities while differing but little in morphological characters, we must also add *Leptogenys*, with its subgenus *Lobopelta*, a rather large tropicopolitan congeries of species belonging to the primitive Ponerine subfamily.¹

Only a single member of this genus, *Leptogenys* (*Lobopelta*) *elongata* Buckley, is known to occur north of the Rio Grande River. It is not uncommon in the semiarid regions of Central Texas (Travis and Comal counties) and has been taken even as far north as Colorado and the District of Columbia. Frequent observations during the past three years have enabled me to confirm and extend my former account of the habits of this very interesting ant.²

I am now able to state positively that the peculiar apterous females, indistinguishable from the workers except for the shorter and more rounded petiolar node and the more voluminous gaster, are the only females produced in the colonies of *L. elongata*. Each colony contains only a single one of these females and no other is tolerated in the nest. Even the young virgin females leave the formicary very soon after hatching and acquiring their

¹ *Lobopelta* differs from *Leptogenys sensu stricto* in having broader mandibles which, when closed, leave little or no space between their inner borders and the anterior margin of the clypeus.

² "A Study of Some Texan Ponerinæ," BIOL. BULL., Vol. II., No. I, Oct., 1900.

red adult coloration. There can, of course, be no true nuptial flight, since the females are wingless. Most conclusive evidence in regard of the nature of these females has been furnished by my former pupil, Miss Margaret Holliday,¹ who found them to possess not only well-developed ovaries but a typical receptaculum seminis. It is interesting to note that the slight morphological differences separating these females from the workers are still further diminished by Miss Holliday's discovery that the latter have as many ovarian tubules as the former and may occasionally possess a receptaculum.

That the numerous tropical species of *Leptogenys* agree with the Texan species in having very ergatoid females, is indicated, first by the fact that no winged *Leptogenys* females have been seen, though many species of the genus have been known for years, and secondly by Wroughton's observations on the Indian *Leptogenys diminuta* Smith, recorded by Forel:² "At my request Mr. Wroughton has excavated an enormous formicary of *L. diminuta* to a considerable depth, but has looked in vain for a female among the many thousands of workers. All he could find was a worker whose abdomen was conspicuously distended with the ovaries. This worker differed in absolutely no particular from the others, and there is nothing very extraordinary even about its abdomen. This result would seem to confirm Emery's opinion."³

In my paper on the Texan Ponerinæ I failed to furnish conclusive proof of the identity of the males of *L. elongata*, as up to that time I had not taken this sex in the formicaries. More recently I have repeatedly seen the males in the natural nests and have bred them from larvæ and cocoons in captivity. They are of a rich yellow color, retaining throughout life the tint exhibited by the workers and females only during their callow stages. Even when quite mature the males are seized by the workers, when-

¹ "A Study of Some Ergatogynic Ants," *Zool. Jahrb. Abth. f. Syst.*, Bd. XIX., Heft 4, 1903, pp. 295-297.

² "Les Formicides de l'Empire des Indes et de Ceylan," Part VII., *Journ. Bombay Nat. Hist. Soc.*, Vol. XIII., p. 312.

³ Emery advanced the opinion that in the genus *Leptogenys* the function of the females may have been usurped by the workers. This is not strictly true, at least in *L. elongata*, since the petiole of the female is clearly different from that of the worker, as it is in the winged females of many other species of Ponerinæ.

ever the nest is disturbed, and carried away like the very slender larvæ and cocoons, with their bodies tucked away between the legs of the workers. The males leave the nests at night, like the peculiar males of *Eciton* — another genus in which the females are apterous — and are often lured into the houses by the electric lights during the late spring and early summer months, especially during the latter part of May and early June. It would be extremely interesting to learn something of the mating habits of these highly heliotactic males and wingless females. Do the males, during the breeding season, seek out and enter strange nests of their own species in order to fecundate the virgin females? This seems improbable when we stop to consider that male ants are so very stupid that they are unable to find their way back to their parental nest when once they have strayed away from it. Are the wingless females fecundated by the males of the same colony, *i. e.*, by the offspring of the same mother? This is possible but improbable, since this would be a flagrant case of inbreeding. It seems more likely that the virgin females leave the parental nest and wander about as pedestrians, till they are found and fecundated by the winged males, as in the case of the Mutillidæ. The same problems and answers seem to be suggested by the large winged males and dichthadiiform females of *Eciton* and *Dorylus*.

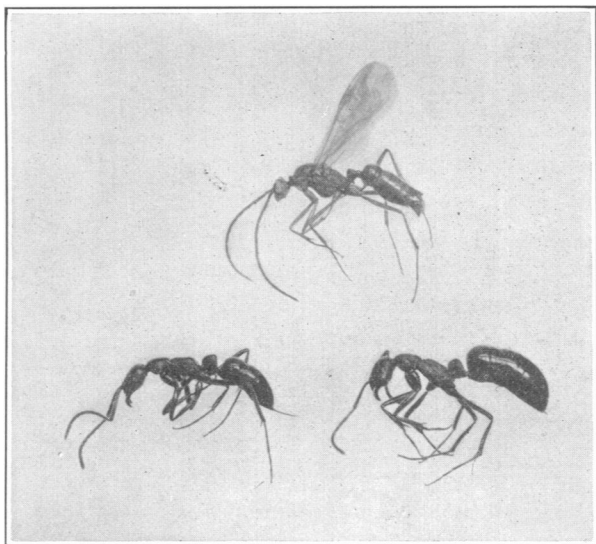
My former paper contained no account of the feeding habits of *L. elongata* in a state of nature. In my artificial nests the insects and their larvæ were fed on termites. I have since found that these ants, under natural conditions, feed very largely, if not exclusively on the common wood-slaters (*Oniscus* and *Armadillidium*) which abound under stones and logs in the shady places where the formicaries are excavated. I have repeatedly seen workers of *L. elongata* returning to their nests, carrying dead slaters in their mandibles. The earth surrounding the entrances to the nests is invariably white with innumerable bleaching limbs and segments of the crustaceans, showing that great numbers of these animals must be habitually destroyed by the ants. Their long, toothless mandibles resemble scissors and seem to be admirably adapted for cutting through the intersegmental membranes of their prey and exposing the

edible parts. *L. elongata* is, to my knowledge, the only ant known to feed on crustaceans as a regular diet. Other ants are either insectivorous, granivorous, mycetophagous, or collectors of the saccharine exudations or juices of insects and plants.

The little that is known concerning the habits of other species of *Leptogenys* would indicate that the North American form is peculiar in the character of its food. Wroughton has studied the habits of two of the Indian species of *Lobopelta*, *L. distinguenda* Emery and *L. chinensis* Mayr.¹ Concerning the former he writes as follows: "This species is fairly common from Poona westwards to the Ghats. The idea of a disciplined army has been fairly developed in this genus. *L. distinguenda* may sometimes, it is true, be found loafing about singly, but these individuals are probably only scouts; ordinarily, she is only met, in the early morning or late in the afternoon, travelling in an unbroken column four to six or eight abreast, straight, or rather by the easiest road, to the scene of operations. This is usually a colony of white ants whose galleries have been broken open by the hoof of a passing beast, or some similar accident. Arrived at destination, each worker seizes her termite prey, tucks it under her thorax in the orthodox ponerine fashion, and the column then returns (but marching 'at ease' and much less regularly than on the outward journey) to the nest. I have never succeeded in finding a nest; on one occasion I tracked a column for more than fifty paces, only to lose it in a patch of prickly pear. I do not think that *L. distinguenda*, any more than any other ant, ever has the inspiration to open a termite gallery for herself; on the occasion mentioned above, the column passed close to several, and even over one colony of white ants before reaching its destination; I believe, however, I saw a worker break open a piece of tunnel, into which a termite had retreated, but cannot be sure, and the practice certainly was not general. Nor are the termites followed into the galleries, partly, perhaps, because the passage is too small for a *Lobopelta*, but equally, I imagine, because such a measure would be very like 'drawing' a badger 'only more so.' Mr. Aitken tells me he has seen 'hundreds going into a hole in the ground and emerging with white ants,' but this is very different from entering a termite gallery."

¹ "Our Ants," *Journ. Bombay Nat. Hist. Soc.*, 1892, p. 56-58.

Concerning *L. chinensis* Wroughton makes the following statements: "This species is even commoner than the last. *Distinguenda* would seem to be a denizen of forests, while *Chinensis* prefers more open and inhabited country. I have only once seen *Chinensis* on the warpath, and then the objective, a large worm, in several pieces, had been reached, and the column was on its way home. The column I must say was more a mob than a disciplined army, but this may have been due to the fact that the normal irregularity of the homeward march was enhanced by the size and shape of the booty, which did not admit



Leptogenys (Lobopelta) elongata Buckley, male, female and worker.

of being carried 'according to the regulations.' On the other hand, I have often, during the early part of the rains, witnessed a migration (or was it a colonization, in no case was a female, even apterous, present?) when the discipline and regularity of the column left nothing to be desired. My experience seems to show that *Chinensis* prefers a formation in fours, at any rate when carrying her own larvæ and pupæ. Mr. Aitken has furnished me with the following most interesting note on *Chinensis*. 'There is a populous community of this ant, in a hole, in the

foundations of my house, at Goa. From the nest there is a well marked "road," crossing a broad gravel path, and then ramifying all over the tennis ground. They issue after sunset, and march along one of the main branches, or break up into parties and take different routes. When they come to a place where the termites have thrown up new earthworks, and are busy eating the dead grass underneath, they collect in dense masses, waiting for an opportunity of breaking in, which they very likely find when the termites attempt to extend their works on any side. Then the slaughter begins. Sometimes the poor termites are killed far faster than they can be carried off; and on one occasion, as late as 7 a. m., I saw the ground still heaped with slain, and an unbroken stream of ants, fifty-six yards long, carrying them away. Each ant had two or three in her jaws. If these ants cross the grounds of a community of 'harvesters' (? *Holcomyrme*) after the latter are up in the morning, they have to flee in their turn. A *Lobopelta*, when once a worker major has laid hold of her by the leg, appears to be perfectly helpless, she can neither kill her enemy nor shake her off. Sometimes another *Lobopelta* will come to her assistance, and, after vainly trying to tear off the aggressor, will pick up her comrade and carry her and her enemy off together.'"

Apparently some of the American species of *Leptogenys* also prey on termites. The nest of a single colony of *L. Wheeleri* Forel which I observed at Cuernavaca, Mexico, was almost embedded in a *Eutermes* nest, and I have no doubt that the ants were in the habit of using their neighbors as a convenient larder.

The only other *Leptogenys* of which I find the habits recorded is *Lobopelta diminuta* Smith var. *bismarckensis* Forel from the Bismarck Archipelago. Dahl¹ compares this species with the amazon ant (*Polyergus rufescens* of Europe and North America). on account of the sickle-shaped, toothless mandibles. He says: "Although I have drawn a comparison between *Leptogenys bismarckensis* and *Polyergus rufescens*, I must clearly emphasize the fact that I never found the nest of the former species and

¹ "Das Leben der Ameisen im Bismarck-Archipel, nach eigenen Beobachtungen vergleichend dargestellt," Berlin, R. Friedländer und Sohn, 1901, p. 52.

could not, therefore, observe whether the work of the colony is carried on by slaves. What firmly convinced me, nevertheless, that this species is a slave-holding ant, was the following: The mandibles are long and sickle-shaped, almost as much so as in our German slave-holders, and little adapted for working, as they have no masticatory border. They could of course, be of use in killing termites, as Forel supposes to be the case in this genus, but the place where I found the species under consideration was far removed from all termite nests. It was on the sea-shore between blocks of coral, where I saw about fifty individuals in a troop, as it were, on the march. It was evident that the troop had left the nest for the purpose of perpetrating a robbery in common. That this robbery, after what has been said, was for the purpose of obtaining slaves, seems probable." I venture to maintain that Dahl is mistaken in supposing that *L. bismarckensis* is a dulotic ant, as a perusal of the above quoted passages from Wroughton's work will suffice to show.

It is also evident from the observations of Wroughton and Aitken that the Indian species of *Leptogenys* differ widely in habit from *L. elongata*. The colonies of the latter species are very small, rarely containing more than a hundred individuals, whereas the colonies of the Indian species appear to contain thousands of workers. Moreover, the workers of *L. elongata* leave the nest singly and hunt about timidly for their phlegmatic and defenceless prey, whereas the Indian species hunt in well organized files somewhat after the manner of the driver ants and ants of visitation (*Dorylus* and *Eciton*). And such diversity of instinct is exhibited not only in the same genus but within the confines of the same subgenus (*Lobopelta*).

In conclusion I give the synonymy and a description of all three phases of the North American *Leptogenys*.

LEPTOGENYS (LOBOBELTA) ELONGATA (Buckley) Wheeler.

Ponera elongata Buckley, Proc. Ent. Soc. Phila., Vol. VI., 1866-67, p. 172, ♀.

? *Ponera texana* Buckley, *ibid.*, p. 170, ♀.

Lobopelta septentrionalis Mayr., Verhandl. k. k. zool. bot. Ges. Wien, Bd. 36, 1886, pp. 438, 439, ♀.

Leptogenys septentrionalis Emery, Zool. Jahrb. Abth. f. Syst., Bd. 8, 1894, p. 268, ♀.

Leptogenys (Lobopelta) elongata (Buckley) Wheeler, Biol. Bull., Vol. II., No. 1, Oct., 1900, p. 2, 7, Fig. 4. ♀ ♂; Trans. Tex. Acad. Sci., Vol. IV., Pt. II., No. 2, 1902, p. 9.

WORKER. — Length 5-6.5 mm.

Head slender, excluding the mandibles, longer than broad, somewhat broader in front than behind. Eyes moderate, flattened, situated a little in front of the middle of the sides of the head. Mandibles slender, nearly two thirds as long as the head, gradually increasing in breadth as far as their apical third, forming a sharp, toothless blade and thence narrowing more suddenly to the acute, curved tip. Clypeus prolonged forward in the middle to a rather acute point and with a prominent median keel; lateral emarginations distinct but not very deep. Frontal furrow extending back a little beyond a line connecting the posterior orbits of the two eyes. Antennæ slender; scapes extending about one third their length beyond the posterior corner of the head. First and third funicular joints subequal, decidedly shorter than the second joint; joints 4-11 subequal, shorter than joints 1 and 3. Thorax elongate, its dorsal surface horizontal, meso- and epinotal regions laterally compressed; depression behind the small mesonotum short but rather deep. Basal surface of epinotum twice as long as the sloping declivity, which is somewhat flattened and transversely margined below and behind. Petiole in profile as high as the thorax, somewhat higher behind than in front and nearly as long as high; anterior, dorsal and posterior surfaces flattened; the dorsal and posterior meeting at a somewhat sharper angle than the anterior and dorsal surfaces. There is a distinct tooth at the anterior, ventral border of the petiole. Seen from above this segment is pyriform, twice as broad behind as in front, with flattened sides and rounded dorsal surface. Gaster slender, somewhat deeper than the petiole, distinctly constricted between the first and second segments. Sting prominent. Legs long and slender; claws with long pectination.

Mandibles smooth and shining, the former with a few scattered punctures and faint traces of striation; the latter thin and submembranaceous along its anterior border and obliquely rugose on the sides. Head, thorax and petiole subopaque, rather densely and uniformly covered with shallow punctures. Region between the eyes and clypeus longitudinally rugose. Gaster shining, very sparsely and finely punctate.

Body and appendages clothed with delicate, grayish yellow pubescence; the head, thorax and abdomen also with sparse, grayish yellow hairs, which are long and projecting on the clypeus and terminal segments of the gaster.

Deep red; edges of mandibles and thoracic sutures somewhat blackened. Antennæ and legs a little paler than the trunk; tip of gaster, sting, anterior border of the clypeus and the spines of the tibiæ, yellow.

FEMALE. — Length 6.5-8 mm.

Apterous and decidedly ergatoid in form, indistinguishable from the

worker in the head and thorax, even lacking ocelli and with eyes no larger than those of the worker. The petiole is proportionally shorter and higher, so that when seen from above, it is little if any longer than broad behind, shaped like an equilateral triangle with rounded angles. In some females the upper surface of the segment in profile is flattened like that of the worker, but in most cases it is more convex and in this respect somewhat like the petiole of the male. Gaster conspicuously larger, both broader and higher than that of the worker. Sting like that of the worker.

MALE. — Length 5.5–6.5 mm.

Head, including the very prominent, somewhat reniform eyes, distinctly broader than long; cheeks and postocular regions very short, ocelli large and protruding. Mandibles small, hardly meeting with their tips, slightly geniculate, broadest at the base and suddenly tapering to a slender point. Clypeus less produced, less pointed in front and with a blunter keel than in the worker. Antennæ long and filiform, 13-jointed; joints 3–13 long and cylindrical, subequal; scape very short, hardly a third as long as the third and succeeding joints; second joint very small, somewhat narrower than the scape and hardly longer than broad. Thorax rather robust, with prominent Mayrian furrows on the mesonotum; epinotum long and sloping. Petiole small, hardly half as high as the first gastric segment, about as high as long, in profile rounded above, with sloping anterior and posterior surfaces; seen from above it is oblong, a little longer than broad, hardly wider behind than in front. Gaster with well developed constriction between the first and second segments and large, cultriform, exerted genital appendages, which are fully half as long as the remainder of the gaster. Legs long and slender.

Smooth and shining, except the antennæ, which are opaque. Surface of thorax indistinctly and finely punctate.

Body covered with yellowish hairs, which are long and prominent on the gaster, shorter on the head and thorax, and still shorter and denser, and more like pubescence, on the appendages.

Body and legs light yellow throughout. First and second antennal joints yellow, remaining joints brown. Wings grayish hyaline with brownish veins and stigma.

Type Locality. — Austin, Texas.

Other Localities. — District of Columbia (Pergande, Mayr); Colorado (Cresson, Emery); New Braunfels and Belton, Texas (Wheeler).